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Research Article
Water Deficit During the Vegetative Stage Alters the Structure of Root-Associated Microbial Communities in Local North Sulawesi Rice

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Abstract
Background and Objective: Changes in rhizosphere microbial populations have been reported in response to drought, temperature fluctuations, CO_2 levels and other environmental factors. However, the structure of the root-associated microbes in local North Sulawesi rice using a metagenomic approach has not yet been investigated. This study examined the microbial community structure in local North Sulawesi rice (cv. Superwin) under drought (water deficit) conditions compared to well-watered conditions at the vegetative phase. **Materials and Methods:** Rice plants were grown in polybags filled with a 5:1:1 mixture of garden soil, compost and rice husks and were allowed to grow until the four-fully-expanded leaf stage. They were then subjected to two treatments for 14 days: well-watered conditions (irrigated to 100% field capacity) and water deficit conditions (0% field capacity). Root samples were collected for next-generation sequencing analysis to assess molecular response of Superwin rice to water deficit. **Results:** During drought, several root-associated microbes were more prevalent, including *Nitrospirota* at the phylum level, *Rubrobacteria* at the class level, *Micrococcales* at the order level, Gaiellaceae at the family level, *Gaiella* at the genus level and *Gaiella occulta* at the species level. **Conclusion:** Root-associated microbes, including taxa *Nitrospirota*, *Rubrobacteria*, Micrococcales, Gaiellaceae, *Gaiella* and *Gaiella occulta*, have a higher relative abundance in rice plants under water deficit. *Gaiella occulta* serves as sensitive indicator of water deficit in North Sulawesi local rice, i.e. Superwin.

Key words: Abundance, diversity, drought, local rice, microbiome

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Competing Interest: The authors have declared that no competing interest exists.

Data Availability: All relevant data are within the paper and its supporting information files.

INTRODUCTION

Superior cultivars can enhance agriculture productivity through both intensification and extensification, as they can adapt to specific conditions, outperforming wide-adaptive varieties[1,2]. The Indonesian Ministry of Agriculture's Food Security Movement aims to strengthen food reserves and logistical systems by increasing rice stocks, implementing adaptation measures like changing planting times, utilizing drought-resistant varieties and developing water management technologies[3]. Sulawesi, Indonesia's third-largest rice producer, has the potential to become a rice farming center due to its diverse native rice cultivars, such as Superwin[4].

Drought significantly impacts food crops by reducing productivity, primarily due to damage to photosynthetic enzymes and increased accumulation of reactive oxygen species caused by impaired antioxidant machinery[5]. Drought-resistant cultivars, on the other hand, counter these effects by storing dissolved sugars, proline, glycine betaine, K^+ and other solutes, allowing physiological systems to function normally[6]. Drought triggers hormonal signaling pathways controlled by abscisic acid and jasmonic acid, prompting plants to close stomata, limit K^+ uptake and reduce transpiration rate[5]. The drought response in Superwin rice from North Sulawesi has been studied using morphological traits such as plant height, leaf number, root length, root to shoot ratio, water content, chlorophyll content, K^+ concentration, glycinebetaine and proline[4,6-10]. Superwin was reported as a semi-tolerant rice cultivar based on physiological characteristics[7]. Despite the findings, the metagenomic approach to molecular analysis of drought resistance traits in North Sulawesi rice has not yet been explored.

Soil microorganisms, both beneficial and harmful, accumulate in the rhizosphere and affect plant growth, development and health through interactions with bacteria communities and roots[11]. Understanding the composition of microbial the plants during drought is a valuable genetic resource for enhancing plant resistance[5,9,12-14]. Numerous studies have reported changes in the rhizosphere microbial populations in response to drought, temperature fluctuations, CO_2 levels and other environmental factors[15,16]. Studies have shown that plants adapt to stressful conditions due to increased microbial populations and analyzing the root microbiome can provide insight into vital ecosystem functions[15-18]. This study investigated the microbial population structure in North Sulawesi rice under drought (water deficit) conditions, focusing on the specific microbes as bioindicators of water deficit in Superwin rice.

MATERIALS AND METHODS

Location and duration of study: The study was carried out in Manado, North Sulawesi, Indonesia from June to November 2023.

Experimental design and treatment: This Completely Randomized Design experiment, featuring two treatments and three replications, was carried out in a greenhouse with local North Sulawesi rice types, specifically Superwin. This experiment involved preparation, treatment, data collection and analysis. Preparation procedures included preparing rice seedlings and planting medium in polybags, planting the seedlings and maintaining the plants. Rice was sown in polybags with a mixture of garden soil, compost and rice husks (5:1:1) and allowed to grow until the rice plants had four completely grown leaves before the treatment. Drought was imposed during the vegetative phase for 14 days, using two treatments: Well-watered (irrigated to 100% field capacity) and water deficit (0% field capacity)[6]. The response of Superwin rice to water deficit was evaluated molecularly by metagenomic analysis using root samples.

Data collection: Metagenomic analysis was used to determine the structure of the microbial community surrounding plant roots, which serves as a habitat for a diverse range of beneficial and harmful microorganisms. After the drought treatment was completed, root samples were collected from both well-watered and water-deficient plants. Before sampling, any stones, rubbish, or grass were removed from the soil's surface. Furthermore, top-soil samples were collected at a depth of 0-20 cm using a sterile shovel, while root samples were obtained by uprooting the plant. The roots were aggressively shaken by hand to remove the bulk soil[19].

Data analysis: The diversity of microorganisms associated with Superwin rice roots was investigated using the next-generation sequencing (NGS) approach. The NGS method was based on amplicon sequencing, which relies on the amplification of phylogenetic marker genes, specifically RNA genes from the small subunit of the ribosome (16S rRNA), followed by bioinformatics analysis[19]. DNA concentration was measured using both Nanodrop spectrophotometers and a Qubit fluorometer. Library preparations were carried out using Oxford Nanopore Technology (ONT) Kits. ONT offers a quick, cost-effective, high-throughput sequencing technology that provides long-read sequencing encompassing the full-length sequence of the 16S rRNA gene (V1-V9). These full-length 16S rRNA sequences enhance taxonomic and phylogenetic

precision for bacterial identification by utilizing all informative regions of 16S rRNA genes[20]. Nanopore sequencing was operated by MinKNOW software version 23.04.5. Base calling was performed using Guppy version 6.5.7 with high accuracy model[21]. The quality of FASTQ files were visualized using NanoPlot and quality filtering was performed using NanoFilt[22,23]. Filtered reads were classified using Centrifuge classifier[24]. The Bacteria and Archaea index was built using NCBI 16S RefSeq database[25]. Downstream analysis and visualizations were performed using Pavian[26].

RESULTS

Relative abundance: The study analyzed the relative abundance of microbial taxa in rice Superwin under water deficit and well-watered conditions. The top ten phyla were *Pseudomonadota*, *Actinomycota*, *Bacillota*, *Acidobacteriota*, *Planctomycota*, *Myxococcota*, *Bacteroidota*, *Verrucomicrobiota*, *Thermodesulfobacteriota* and *Nitrospirota*. Phylum *Actinomycota* was 38% more abundant in WD than in WW (Fig. 1a, Table 1). *Alphaproteobacteria* were the dominant class, followed by *Gammaproteobacteria*, Bacilli, *Actinomycetes*, *Betaproteobacteria*, *Vicinamibacteria*, *Planctomycetota*, *Terriglobia* and *Rubrobacteria*, ranking highest to lowest. Actinomycetes were 1.4 times more abundant under WD than under WW (Fig. 1b, Table 1).

Rhizospheric microbes, including *Hyphomicrobiales*, *Bacillales*, *Vicinamibacteraceae*, *Xanthomonadales*, *Burkholderiales*, *Rhodospirillales*, *Nevskiales*, *Gaiellales*, *Streptosporangiales* and *Micrococcales*, dominated the order composition of rhizosphere microbes in rice Superwin under WD and WW conditions. When compared to WW, WD raised the relative abundance of *Micrococcales*, *Gaiellales* and *Xanthomonadales* by 2.3, 1.8 and 1.7 times, respectively (Fig. 2a, Table 1). *Bacillaceae*, the most abundant family in WD, reached 21.98% and was followed by *Xanthomonadaceae* at 17.47%. In WW, *Vicinamibacteraceae* was the most abundant family at 22.92%. *Gaiellaceae*, *Xanthomonadaceae*, *Paenibacillaceae*, *Phyllobacteriaceae* and *Nitrobacteraceae* had relative abundances that were 1.9, 1.7, 1.4, 1.4 and 1.3 times more under WD than under WW (Fig. 2b, Table 1).

Root-associated microbes in Superwin were abundant in both WD and WW environments. Common genus included *Vicinamibacter, Gaiella, Luteitalea, Thermomonas, Mesorhizobium, Steroidobacter, Rhodoplanes, Bradyrhizobium, Thermomonas and Mesorhizobium.* The relative abundance of *Thermomonas, Mesorhizobium, Bradyrhizobium and Steroidobacter* under WD were 2.1, 1.9, 1.8, 1.1 and 1.1-fold greater than those under WW, respectively (Fig. 3a, Table 1). *Vicinamibacter silvestris*, *Gaiella occulta*, *Luteitalea pratensis*, *Pseudolabrys taiwanensis*, *Methylothermalis aethiopiae*, *Rhodoplanes* sp., *Brevitalea* sp., *Bradyrhizobium* sp. and *Chthoniobacter flavus* were the most common species. *G. occulta* was abundant in WD (22.70%), while *V. silvestris* was abundant in WW (33.83%). WD increased the relative abundance of *G. occulta*, *Brevitalea* sp., *Bradyrhizobium* sp. and *C. flavus* by 2.4, 1.3, 1.3 and 1.2 times respectively, compared to WW (Fig. 3b, Table 1).

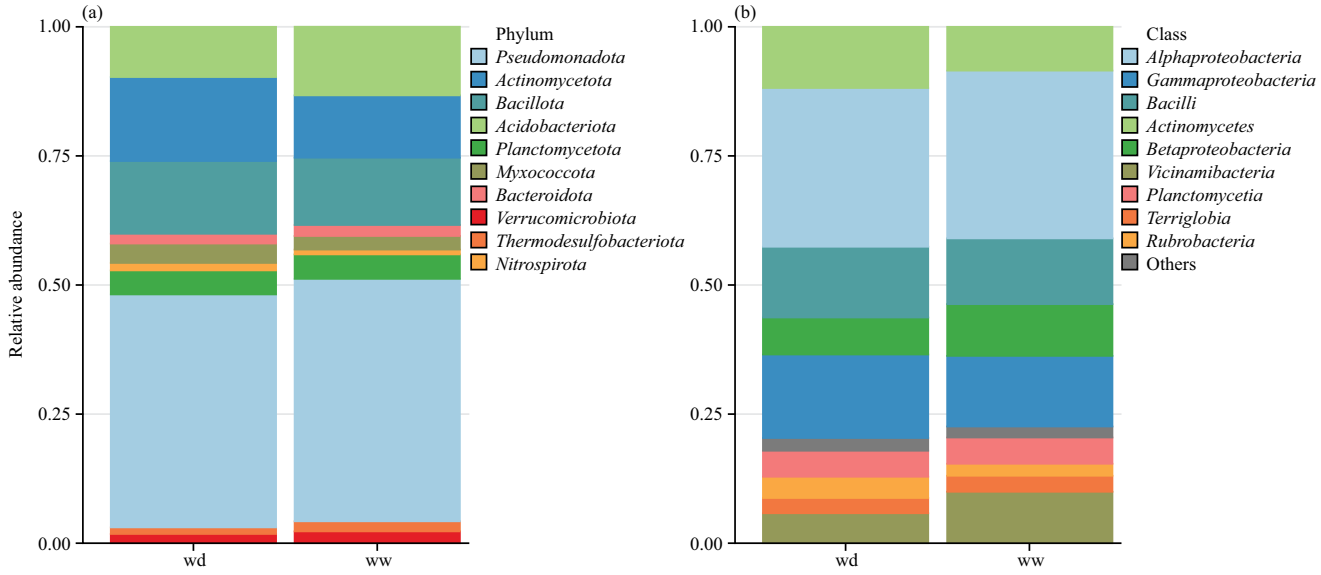

Fig. 1(a-b): Taxa relative abundance at phylum and class levels in local rice Superwin under WD (water deficit) and WW (well-watered) conditions, (a) Taxa relative abundance at the phylum level and (b) Taxa relative abundance at the class level

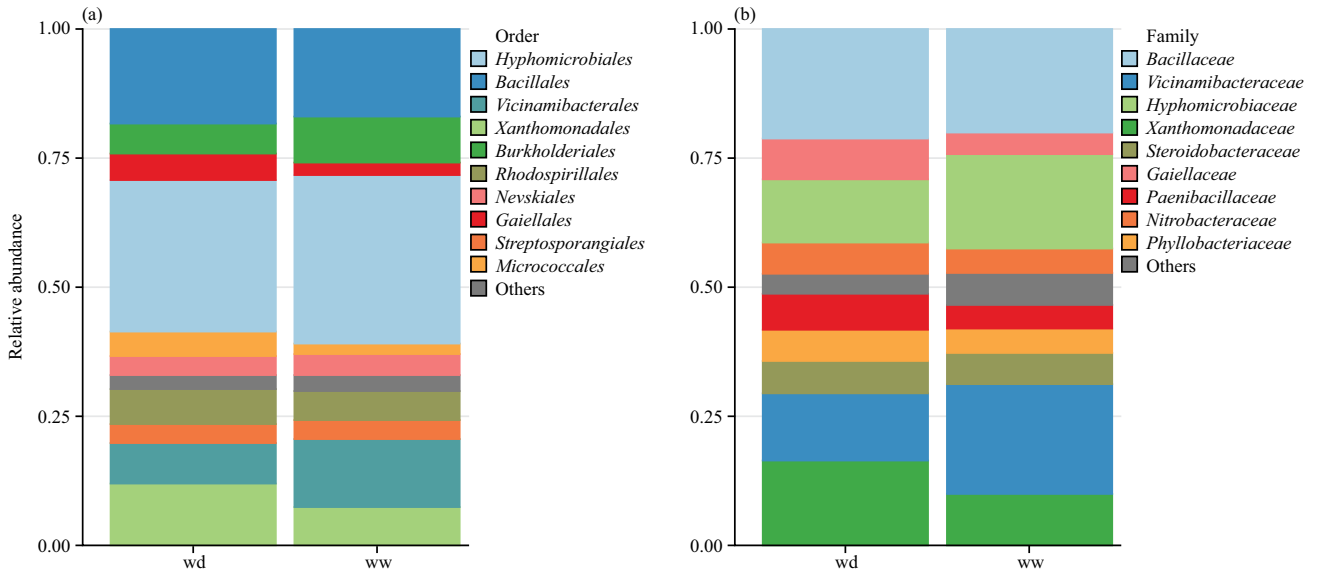

Fig. 2(a-b): Taxa relative abundance at order and family levels in local rice Superwin under WD (water deficit) and WW (well-watered) conditions, (a) Taxa relative abundance at the order level and (b) Taxa relative abundance at the family level

Table 1: Taxa relative abundance at phylum, class, order, family, genus and species in local rice Superwin under WD (water deficit) and WW (well-watered) conditions

	Relative abundance (%)			Relative abundance (%)	
Phylum	wd	ww	Class	wd	ww
Pseudomonadota	45.15	47.06	*Alphaproteobacteria*	31.43	33.32
Actinomycetota	16.48	11.92	*Gammaproteobacteria*	16.62	13.96
Bacillota	13.96	13.08	*Bacilli*	14.01	13.10
Acidobacteriota	9.62	13.34	*Actinomycetia*	12.08	8.68
Planctomycetota	4.52	4.60	*Betaproteobacteria*	7.56	10.23
Myxococcota	3.80	2.80	*Vicinamibacteriia*	5.89	10.16
Bacteroidota	2.07	2.15	*Planctomycetia*	5.28	5.15
Verrucomicrobiota	1.73	2.33	*Terriglobia*	3.14	3.21
Thermodesulfobacteriota	1.33	1.86	*Rubrobacteria*	3.97	2.19
Nitrospirota	1.34	0.86			
	Relative abundance (%)			Relative abundance (%)	
Order	wd	ww	Family	wd	ww
Hyphomicrobiales	30.21	33.47	*Bacillaceae*	21.98	21.44
Bacillales	18.76	17.43	*Vicinamibacteraceae*	13.49	22.92
Vicinamibacterales	8.04	13.82	*Hyphomicrobiaceae*	12.69	19.03
Xanthomonadales	12.41	7.51	*Xanthomonadaceae*	17.47	10.37
Burkholderiales	6.35	9.16	*Steroidobacteraceae*	6.28	6.63
Rhodospirillales	6.81	5.91	*Gaiellaceae*	8.36	4.50
Nevskiales	4.05	4.33	*Paenibacillaceae*	7.02	4.95
Gaiellales	4.98	2.71	*Nitrobacteriacea*	6.29	5.47
Streptosporangiales	3.71	3.57	*Phyllobacteriaceae*	6.43	4.70
Micrococcales	4.68	2.08			
	Relative abundance (%)			Relative abundance (%)	
Genus	wd	ww	Species	wd	ww
Vicinamibacter	20.20	32.67	*Vicinamibacter silvestris*	24.73	35.83
Gaiella	18.55	8.67	*Gaiella occulta*	22.70	9.51
Luteitalea	9.20	10.67	*Luteitalea pratensis*	11.26	11.70
Pseudolabrys	7.17	10.87	*Pseudolabrys taiwanensis*	8.77	11.92
Steroidobacter	9.34	8.65	*Methylothermalis aethiopiae*	7.52	8.50
Rhodoplanes	6.97	10.41	*Rhodoplanes* sp.	5.29	7.18
Bradyrhizobium	8.76	7.44	*Brevitalea* sp.	7.23	5.57
Thermomonas	10.41	5.37	*Bradyrhizobium* sp.	6.76	5.17
Mesorhizobium	9.41	5.26	Chthoniobacter flavus	5.74	4.63

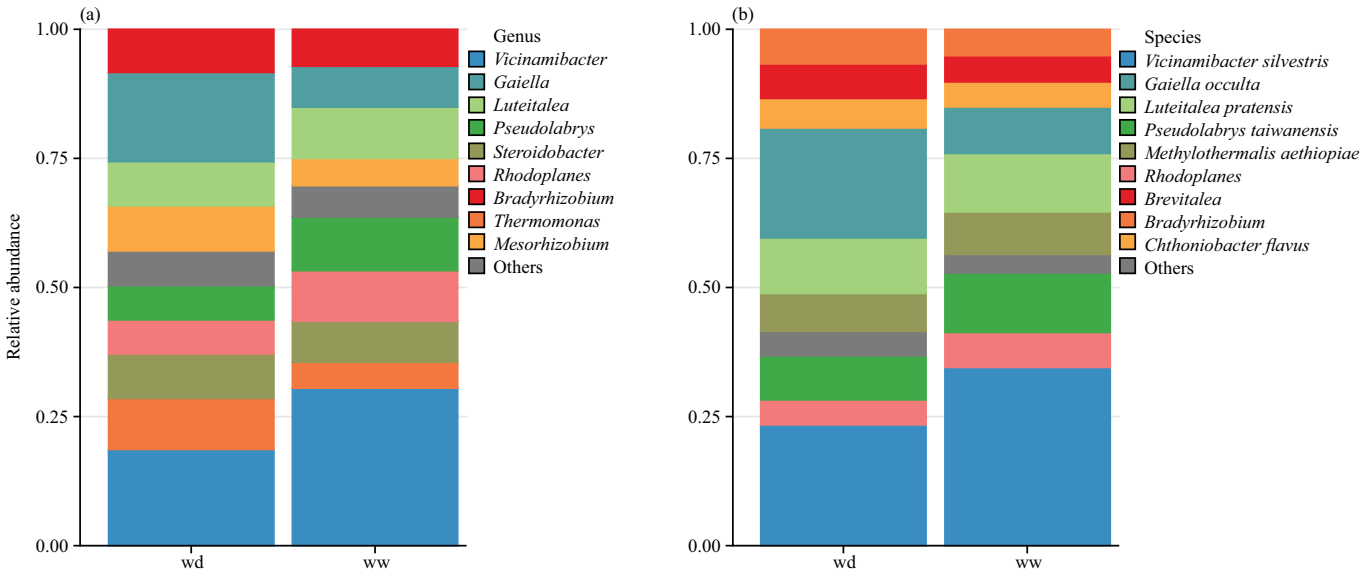

Fig. 3(a-b): Taxa relative abundance at genus and species levels in local rice Superwin under WD (water deficit) and WW (well-watered) conditions, (a) Taxa relative abundance at genus level and (b) Taxa relative abundance at species level

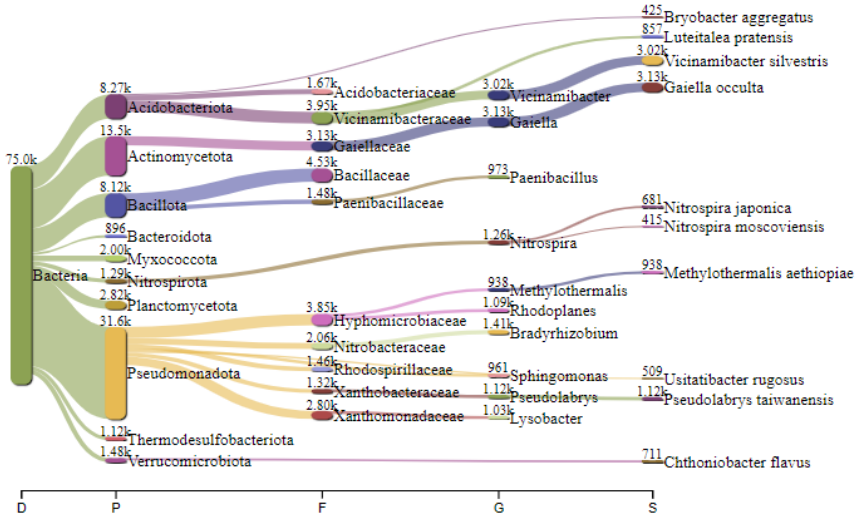

Fig. 4: Sankey diagram illustrated the taxonomic distribution of predominant rhizosphere microbiomes in local rice Superwin under water deficit conditions from division to species levels

The phylum Acidobacteriota included *V. silvestris*, *L. prantensis*, *Brevitalea* sp., while *P. taiwanensis*, *M. aethiopiae*, *Rhodoplanes* sp., *Bradyrhizobium* sp. belong to *Pseudomonadota*. *C. flavus* belongs to *Verrucomicrobiota*, while *Bradyrhizobium* sp. belongs to the *Nitrobacteriaceae* family (Fig. 4). Under WD conditions, Actinomycota, *Nitrobacteriaceae*, *Gaiellaceae* and *Bradyrhizobium* sp. showed increased abundance, with *Bradyrhizobium sp.* being 30.82% more abundant than under WW, Nitrobacteriaceae being 14.90% more abundant, Actinomycetota 38.23% more abundant.

Alpha diversity: Root-associated microbial communities under WD and WW conditions showed higher alpha diversity indices, as reflected by larger Shannon and Simpson indexes indicating large species diversity. The Shannon index prioritizes species diversity and rarity, with rare species receiving more weight. The Shannon index of the root-associated microbial community at WD and WW that are larger than three indicates that the community has a large species diversity. The Simpson index emphasizes species evenness and dominance, giving it more weight than common species. The Simpson index in WD and WW is close

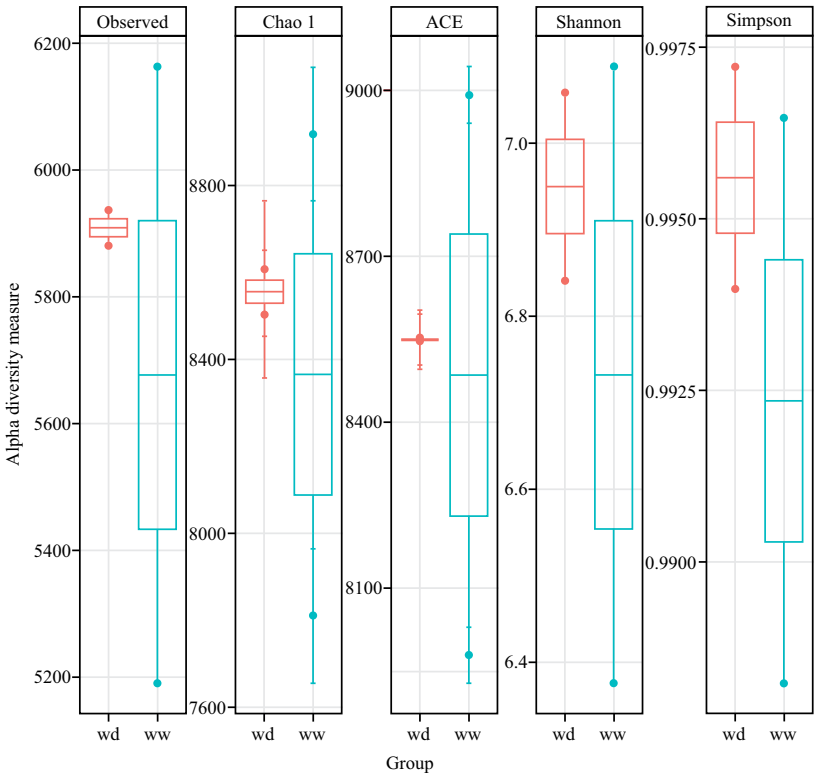

Fig. 5: Alpha diversity of root-associated microbes in local rice Superwin under WD (water deficit) and WW (well-watered) conditions

to one, indicating low microbial diversity. The species diversity in WD was greater than in WW and the species diversity value was more stable than in WW, as evidenced by the standard deviation value in WD being significantly lower than in WW. The WD condition demonstrated higher species diversity and more stable species diversity values, with certain species being more prominent than those in WW condition (Fig. 5).

DISCUSSION

Agricultural systems are greatly impacted by drought, particularly the soil microbiome. Drought-induced alterations disorganized the structure, function and interactions of microbial communities with plants, even though soil microbes are essential for nutrient cycling, plant health and ecosystem stability[27].

A relative abundance ratio of WD to WW greater than one suggests that the taxon is influenced by water scarcity[28]. WD affected various phyla, including *Actinomycota*, *Bacillota*, *Myxococcota* and *Nitrospirota*. *Actinomycetes*, *Gammaproteobacteria*, Bacilli and Planctomycetes were classes affected by the stress. WD affected *Micrococcales*, *Gaiellales*, *Xanthomonadales*, *Rhodospirillales*, *Bacillales* and *Streptosporangiales* at the order level. At the family level, WD affected *Gaiellaceae*, *Xanthomonadaceae*, *Paenibacillaceae*, *Phyllobacteriaceae* and *Nitrobacteraceae*. *Nitrospirota*, *Rubrobacter*, *Micrococcales* and Gaiellaceae were promising microbial taxa for rice plant adaptation to water scarcity.

Gaiella, *Thermomonas*, *Mesorhizobium*, *Bradyrhizobium* and *Steroidobacter* all had abundance ratios larger than one under WD at the genus level. The relative abundance of *Gaiella, G. occulta*, *Brevitalea* sp., *Bradyrhizobium* sp. and *C. flavus* all had abundance ratios higher than one under WD at the species level. *Gaiella* is positively correlated with carbon cycling, secondary metabolite production, soil urease activity, soil accessible N content, plant development and N uptake[29,30]. *Bradyrhizobium* sp., plays a role in carbon cycling and secondary metabolite production[29], while *C. flavus* is crucial in decomposing plant material and transforming organic carbon compounds[31].

Root-associated microorganisms, including bacteria, archaea, fungi, viruses and oomycetes, play a crucial role in plant growth, development and drought resistance[9]. Water deficit alters root exudates, i.e., the compounds released by roots which modify the microbial community, selecting species that help the plant tolerate stress[32]. Through rhizodeposition, these microbes convert dead plant cells and

root exudates into proteins and carbohydrates, contributing to the nutrient cycle and facilitating changes in root architecture during water deficit. They are both environmentally friendly and cost-effective in supporting rice plants during drought conditions[33-35]. Enhancing our knowledge of the dynamics of drought-microbiomes can help develop flexible techniques and sustainable farming methods to lessen the negative effects of drought on crop productivity and ecosystem health[27] as well as select microorganisms that have adapted to drought for use in agriculture[36].

CONCLUSION

It can be concluded that root-associated microbes, including taxa *Nitrospirota*, *Rubrobacter*, *Micrococcales*, *Gaiellaceae*, *Gaiella* and *G. occulta*, have a higher relative abundance in rice plants under water deficit. *Gaiella occulta* is a sensitive, real-time indicator of water deficit in Superwin as a North Sulawesi local rice. While water deficit significantly altered root-associated microbial communities in Superwin rice, their specific role in enhancing rice resistance, especially during water deficit, requires further investigation.

SIGNIFICANCE STATEMENT

The results of this study regarding the structure of the root-associated microbe community in local North Sulawesi rice, i.e. Superwin, subjected to water deficit at the vegetative stage, are novel because they identify distinct, adapted microbial communities that persist in this local rice. The findings indicate that soil microorganisms, such as *Gaiella occulta*, are particularly abundant in the rhizosphere of North Sulawesi local rice, i.e. Superwin, during water deficit. This root-associated bacterium acts as a biomarker to aid rice plant health during water deficit. This finding is essential for choosing microbial-based drought-tolerant techniques.

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